SHELL DEVELOPMENT IN *SPIRIFER TRIGONALIS* FROM THE CARBONIFEROUS OF SCOTLAND

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ABSTRACT. The neotype of *Spirifer trigonalis* (Martin) is described and a group of spiriferids from the Carboniferous Limestone Series of Lanarkshire, displaying wide variation in external form, is assigned to this species.

The microstructure and distribution of lamellar, fibrous, and inner columnar layers is described. Extracellular secretion of the columnar layer is postulated. Interlayering of fibrous and columnar layers is attributed to pauses in growth, accompanied by retraction of the mantle and a consequent change in distribution of the layers. The distribution and development of internal plates is described. Teeth, dental flanges, delthyrial plate, dental sockets, crura, and cardinal process appear in the neanic shell and continue to grow. The delthyrial plate covers early dental flanges: similarly the cardinal process buries early socket cavities and crural bases. Dental plates appear first in the ephebic shell and contribute to the apical infilling in the adult shell.

SINCE Carpenter (1853, p. 25) described the microstructure of the spiriferid shell and speculated on its mode of origin growth studies have been few, and microstructure has been generally neglected in all but the punctate genera. Only Miloradovitsch (1937) recognized the value of shell structure in reconstructing the general pattern of shell development. The detailed study of the shell in one species, *Spirifer trigonalis* (Martin), has shown that in the microstructure there is much evidence of the ontogeny of the shell and some suggestion of its mode of origin.

As no description of the species has been given since the validation (International Commission 1956) of the name *trigonalis* a systematic description follows.

SYSTEMATIC DESCRIPTION

Family SPIRIFERIDAE King 1846, p. 28
Subfamily SPIRIFERINAE Schuchert 1913, p. 410
Genus SPIRIFER Sowerby 1816, p. 125, pl. 270

Type species *Spirifer striatus* (Martin)

Remarks. The internal characters of the genus are unknown, not being shown in the neotype (International Commission 1956, p. 89). The name *Spirifer* is retained here to signify a costate spire-bearer with transverse form, though *S. trigonalis* differs from *S. striatus* in the details of shell profile, rib and furrow shape, and microsculpture.

Spirifer trigonalis (Martin)

Neotype—Plate 64, 1–3

The trivial name *trigonalis* was proposed by Martin (1809, pl. 36) in the combination *Conchyliolithus Anomites trigonalis*. Sowerby (1818–21, p. 117, pl. 275) assigned the species to his genus *Spirifer*. Sowerby's interpretation of the species, however, differed from Martin's original description. When, by the ruling of the International Commission on Zoological Nomenclature (1950), *trigonalis* was invalidated, Muir-Wood (1951)

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considered it undesirable to refer *trigonalis* to Sowerby and permission was sought and obtained from the International Commission (1956) to validate *trigonalis* Martin 1809.

Neotype. Since the type specimen illustrated by Martin (1809, pl. 36) is lost a neotype was selected (International Commission 1956, pp. 112–13). It is a specimen in the British Museum (Natural History) BB 7340 (plate 64, 1–3) which was figured by Davidson (1858, pl. 5, fig. 33 and 1863, pl. 50, fig. 4).

Occurrence. The neotype is from the North Greens Limestone of the Lower Limestone Group, Carboniferous Limestone Series, at Cousland, Dalkeith, Midlothian. The species is thus no longer based on material from Derbyshire.

Diagnosis. Martin's (1809) original diagnosis deals with the general trigonal shape of the shell and the costation of sulcus and flanks. An examination of the neotype and of topotype material in the collections of the Geological Survey, Scottish Office (B 1735d, B 1787d, T 3277F), reveals the following additional characters: the ribs are rounded; very fine longitudinal striations produce a twilling of the growth-lines. Dental plates short, dental flanges present, ventral septum low, convex delthyrial plate in apex of delthyrium (Pl. 65, fig. 7).

Description of neotype

Length	19·8 mm.
Maximum width	23·8 mm.
Hinge width	21·35 mm.
Thickness	12·8 mm.

Shell subtriangular, biconvex, moderately inflated. Width/length ratio 1·2; maximum width anterior to hinge-line, greatest thickness near mid-length. Cardinal angle obtuse. Ventral umbo pointed, overhangs interarea; dorsal umbo low, rounded. Ventral interarea delimited by beak ridges; delthyrium edged by dental ridges, delthyrial plate at apex. Denticle tracks, about twenty-four, underlying lamellar layer. Dorsal interarea low and notothyrium obscured by detritus.

Ventral sulcus wide and shallow, with gently sloping sides and labial extension. Dorsal fold rises sharply from the flanks. Fold and sulcus originate at about 1 mm. from umbo. Anterior commissure uniplicate.

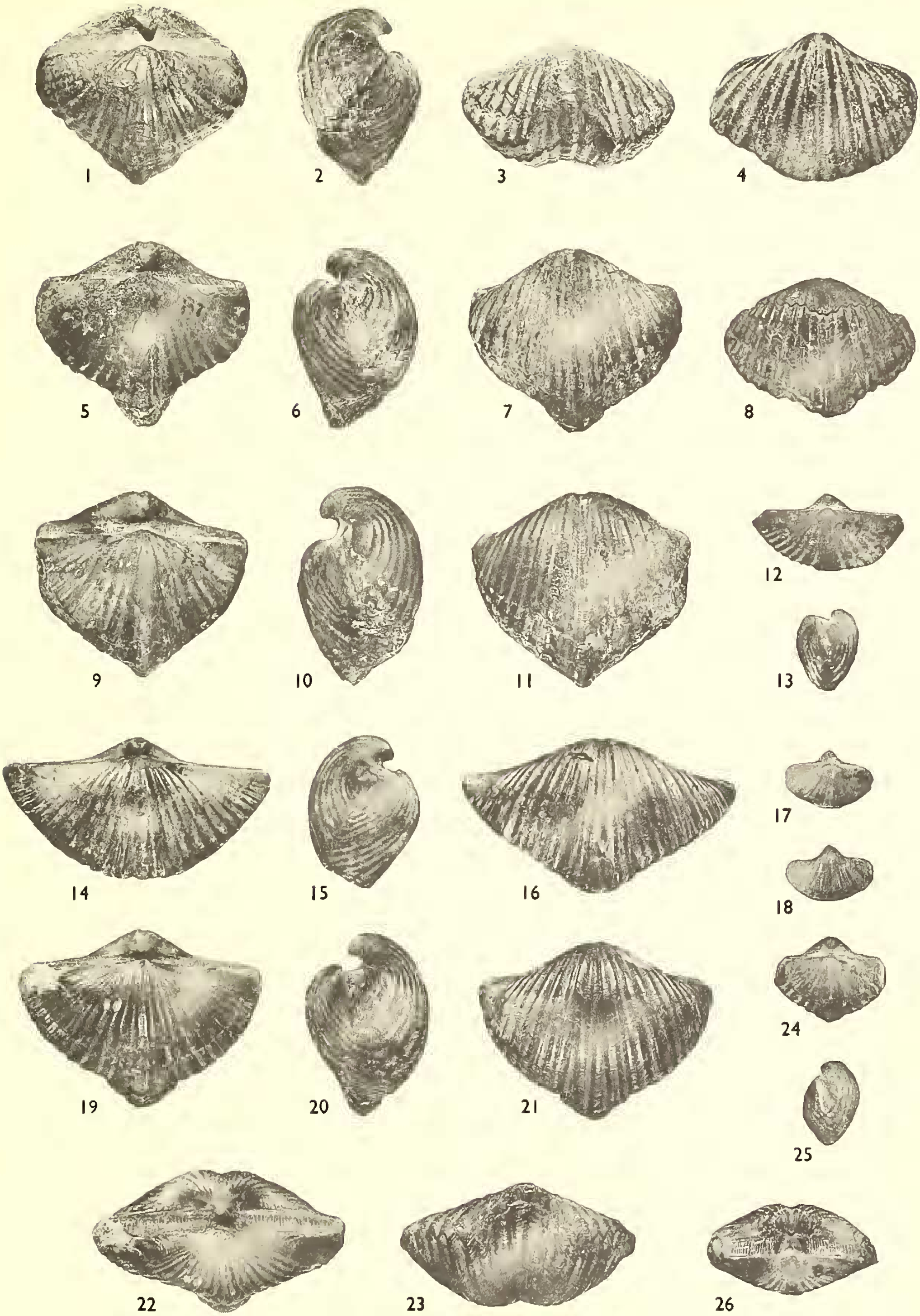
Ribs on flanks, from seven to nine in number, strong, broad and rounded, separated by rounded furrows. Weakly developed incipient ribs at cardinal extremities. The ribs immediately adjacent to both fold and sulcus show dichotomy. Also, the third rib to the right of the dorsal fold, and the corresponding rib in the pedicle valve, divide near the anterior margin.

EXPLANATION OF PLATE 64

Spirifer trigonalis (Martin). All figures natural size, except 4.

Figs. 1–3. Neotype (British Museum BB 7340); North Greens Limestone of Lower Limestone Group; Cousland, Dalkeith, Midlothian. 1, Dorsal view; 2, Lateral view; 3, Anterior view.

Figs. 4–26. *Spirifer trigonalis* (Martin); Douglas Main Limestone of Lower Limestone Group; Brockley, Lanarkshire. All specimens in Hunterian Museum, Glasgow. 4, Ventral view showing many growth-lines. L 3636. 5–7, Dorsal, lateral, and ventral views. L 3633. 8, Ventral view showing four prominent growth-lines. L 3640. 9–11, Dorsal, lateral, and ventral views. L 3632. 12, 13, Dorsal and lateral views. L 3637. 14–16, Dorsal, lateral, and ventral views. L 3635. 17, 18, Dorsal and ventral views. L 3638. 19–23, Dorsal, lateral, ventral, posterior, and anterior views. L 3641. 24, 25, Dorsal and lateral views. L 3639. 26, Posterior view showing denticle tracks on interarea. L 3634.



DUNLOP, *Spirifer trigonalis* (Martin)

In ventral sulcus, two lateral ribs split off from each of the two bounding ribs. A median rib becomes very prominent anteriorly. The ribs on the fold correspond in pattern, with two lateral ribs on each side and a broad central rib with a median furrow.

Many growth-lines visible, two notably prominent and several well marked near anterior margin. Growth-lines also visible on ventral inter-area. No microsculpture is present due probably to the state of preservation of the specimen.

Internal characters are unknown.

Comparison with other species. The field of *Spirifer trigonalis* became widely comprehensive during the nineteenth century with the result that many of the specimens assigned to the species by Davidson (1858–63, pl. 5, fig. 28; pl. 50, figs. 5–8) and de Koninck (1887, pl. 26, figs. 5–8; pl. 28, figs. 7, 27, 31) are quite unlike the neotype both in shape of shell and shape and number of ribs. The specimens recognized as *S. trigonalis* var. *lata* by Schellwien (1892, p. 46, pl. 5, figs. 10–12), Scupin (1900, pl. 9, fig. 7), and Rakusz (1932, p. 72, pl. 2, fig. 34) are probably outside the range of variation of the species.

The Russian specimens described by Trautschold (1876, p. 351, pl. 8, fig. 3), Lebedew (1929, p. 256, pl. 10, fig. 5), and Rotai (1931, pp. 77 and 123, pl. 10, fig. 4) seem to be more closely allied. Schwezow (1925, pp. 156 and 178, pl. 4, fig. 2) recognizes *S. trigonalis* var. *typica* from the Moscow basin which is close to the neotype.

Semichatova (1941, p. 156 in translation) erected the species *S. pseudotrigonalis* for forms which 'could be probably regarded as a local variety of *Spirifer trigonalis*' (p. 157). She shows that there are some small differences in external shape between her specimens and Martin's holotype. Now that the internal characters of the pedicle valve in the topotype material of *S. trigonalis* are known (Plate 65, fig. 7), and it is found that they closely resemble those of *S. pseudotrigonalis* (Semichatova 1941, pl. 8, figs. 1*a*, *b*, 2, 3*a*, 4; pl. 9, figs. 1, 2) in the details of the dental plates, dental flanges, septum and delthyrial plate, the similarity of the two species is more striking and the question of their synonymity arises. *S. pseudotrigonalis*, by original diagnosis (Semichatova 1941, p. 156), has non-dichotomous ribs, whereas the neotype of *S. trigonalis* shows dichotomy; but *S. pseudotrigonalis* var. *furcata* Semichatova (1941, p. 157) is distinguished by 'the bifurcation of plications taking place both in the sinus and on the lateral portions of the shell', and it seems probable that in this wider sense *S. pseudotrigonalis* is a synonym of *S. trigonalis*. In external form *S. pseudotrigonalis* is no less like *S. trigonalis* than are some of the variants of *S. trigonalis* now demonstrated. Indeed several of the other species distinguished by Semichatova (1941), in the *S. pseudotrigonalis* group, on the basis of size, shape, shape of fold and sulcus, and details of rib patterns present a range of variation in external form similar to that now shown in *S. trigonalis* and their validity is therefore doubtful: they may be no more than named variants of *S. trigonalis*.

SPECIMENS FROM BROCKLEY

The specimens used in the study of the development of the shell (Plate 64, figs. 4–26) are from the Douglas Main Limestone of the Lower Limestone Group, in the Poneil Water, at Brockley, $1\frac{1}{2}$ miles south of Coalburn, Lanarkshire. One hundred and seventeen specimens were collected and are now in the Hunterian Museum, Glasgow (figured specimens nos. L 3632–L 3641).

Ninety-six of the specimens are sufficiently well preserved to be studied biometrically. They were all collected from one exposure but they were distributed through about 20 feet of limestone so they cannot be regarded as strictly contemporaneous members of a single population. Also, the presence of separate valves shows that the specimens were probably transported before burial and do not represent successive populations. The specimens show wide variation in shell shape, the variation being continuous (text-fig. 1*b–e*). The statistical measures of the sample are given in Table 1; the high coefficients

TABLE 1. *Statistical measures of the specimens of* Spirifer trigonalis (*Martin*) *in the collection from Brockley, Lanarkshire*

Character	*Number of specimens*	*Range*	*Mean*	*Standard deviation*
Hinge width (mm.)	72	9·5–39·3	20·4	7·46
Maximum width (mm.)	53	11·0–39·3	21·3	6·98
Length (mm.)	72	7·2–28·1	15·6	5·79
Thickness (mm.)	87	5·2–18·2	10·8	3·59
$\frac{\text{Maximum width}}{\text{Length}}$	51	1·11–1·98	1·46	0·179
$\frac{\text{Thickness}}{\text{Length}}$	87	0·59–0·82	0·69	0·0477
$\frac{\text{Number of ribs}}{\text{Length (mm.)}}$	71	0·64–1·89	1·11	0·232

$$\text{Coefficient of correlation } \frac{\text{hinge-width}}{\text{length}} \; 0{\cdot}77$$

$$\text{Coefficient of correlation } \frac{\text{thickness}}{\text{length}} \; 0{\cdot}90$$

of correlation showing that it is probable that a single species is represented. The scatter diagram and the unimodal histograms (text-fig. 1) present the same evidence.

EXPLANATION OF PLATE 65

Microstructure of shell in *Spirifer trigonalis* (Martin).

Figs. 1–3 and 5–7 are thin sections photographed under crossed nicols. Figs. 1–6: specimens from Douglas Main Limestone, Brockley, Lanarkshire.

Fig. 1. Transverse section showing growth-line in columnar layer, ×30.

Fig. 2. Oblique transverse section showing dental flanges and enveloping dental plates, ×36.

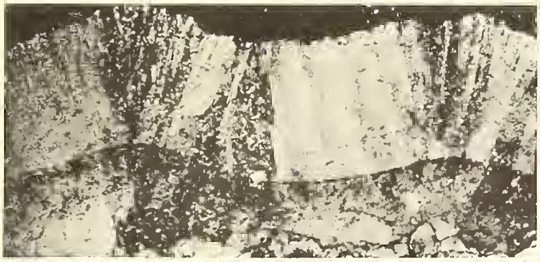
Fig. 3. Longitudinal section showing external lamellar layer and interlayering of fibrous and columnar layers, ×50.

Fig. 4. Cellulose peel of oblique transverse section in apex of pedicle valve showing dental plates and apical infilling, ×40.

Fig. 5. Longitudinal section of ventral interarea showing fibrous and columnar layers and a remnant of lamellar layer, ×25.

Fig. 6. Longitudinal section showing external growth-line and corresponding internal growth-line in fibrous layer, ×17.

Fig. 7. Specimen from North Greens Limestone, Cousland, Dalkeith, Midlothian. T3277F Geological Survey Collections, Edinburgh. Transverse section of pedicle valve showing dental plates, dental flanges, and a remnant of delthyrial plate, ×8.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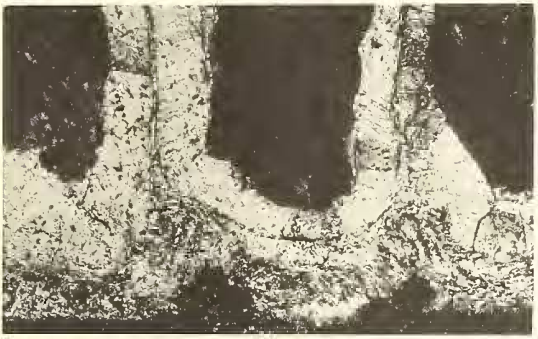
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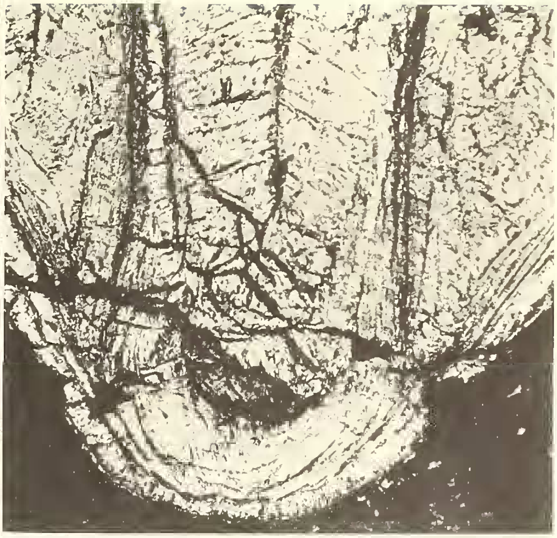
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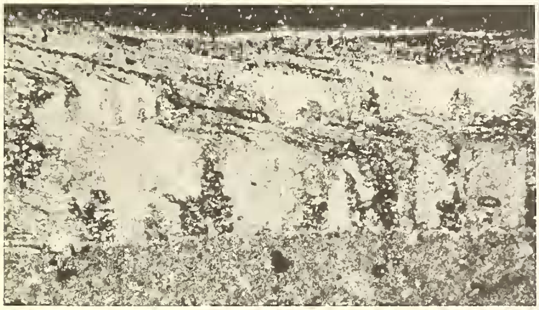
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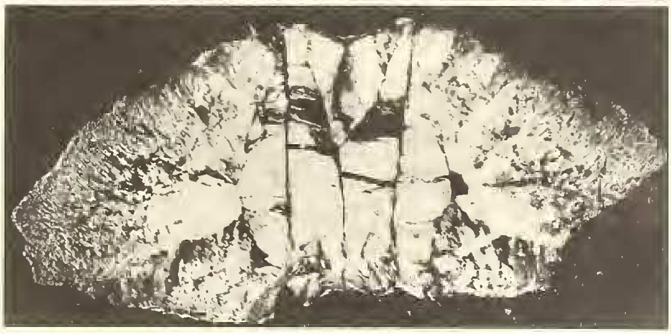
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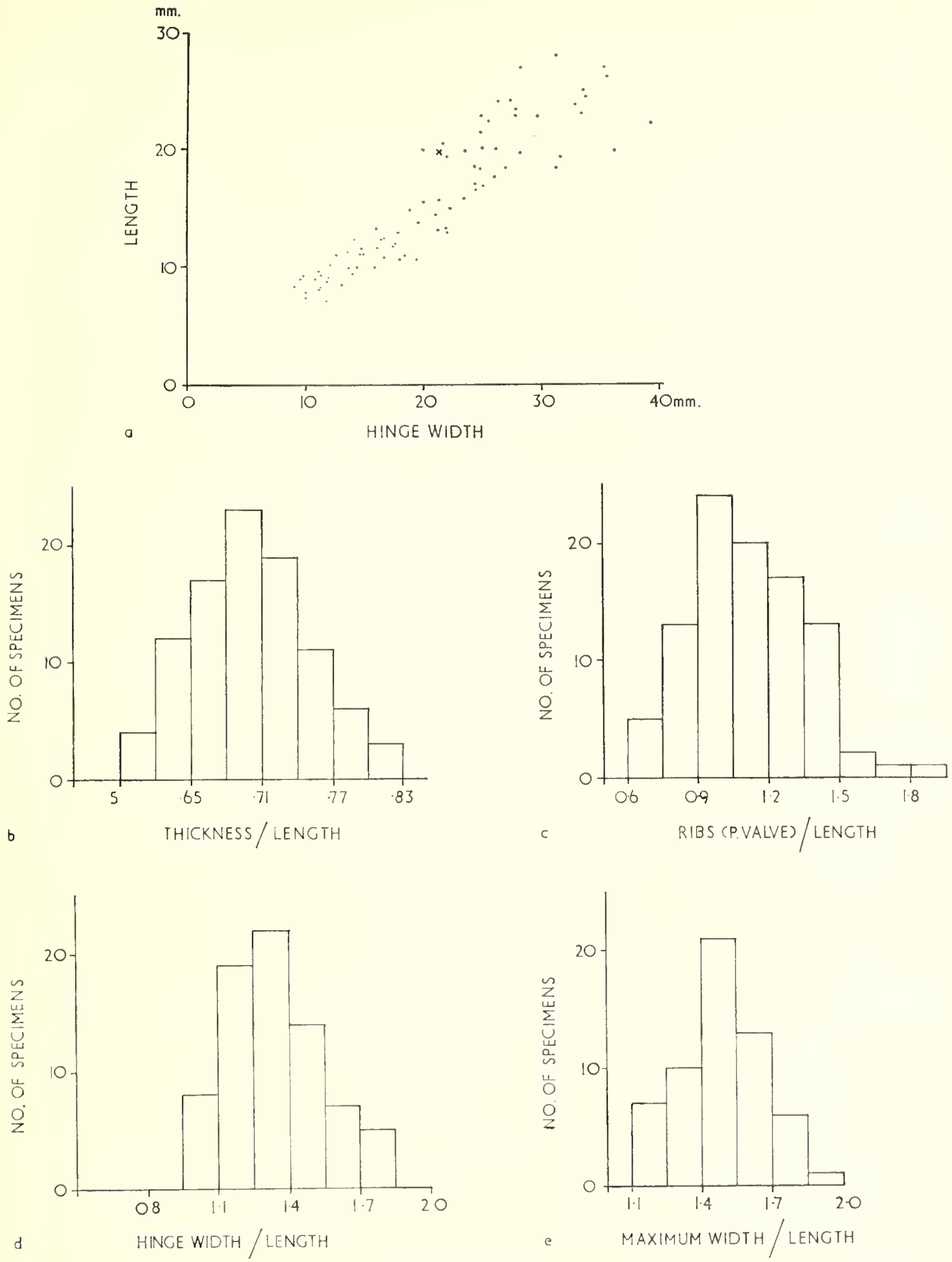
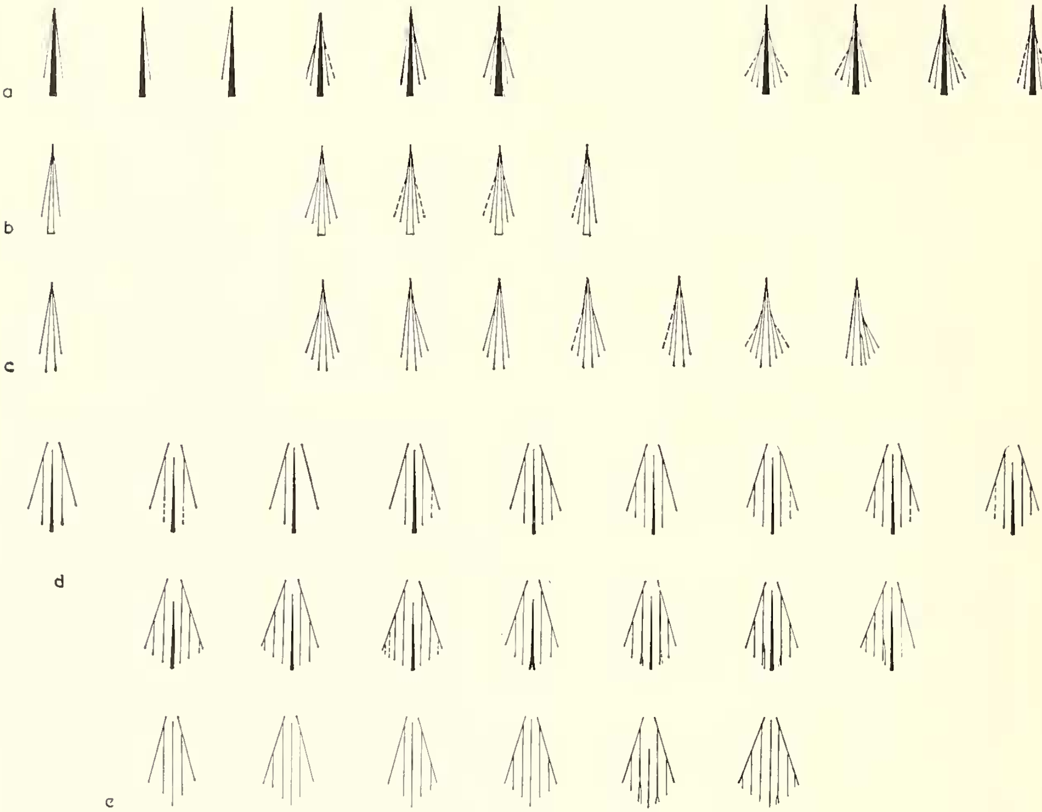


TEXT-FIG. 1. *Spirifer trigonalis* (Martin) from Brockley, Lanarkshire. *a*, Scatter diagram, x = neotype of species. *b–e*, Histograms showing frequency distribution of various shell ratios; *b*, 95 specimens; *c*, 96 specimens; *d*, 75 specimens; *e*, 58 specimens.

Variation in such characters as the number of ribs on fold and sulcus (text-fig. 2), the height and width of fold and sulcus, and the shape of cardinal angles are considered to be intraspecific.

Comparison of neotype with Brockley specimens. When plotted on the same diagram the



TEXT-FIG. 2. Variation in the ribs of fold and sulcus in *Spirifer trigonalis* (Martin). *a–c*, Ribs on fold; *a*, median rib undivided; *b*, median rib with longitudinal furrow; *c*, median rib divided. *d–e*, Ribs in sulcus; *d*, median rib prominent; *e*, median rib not prominent. Broken lines indicate faint ribs, and heavy lines indicate prominent median ribs.

neotype of *Spirifer trigonalis* lies on the fringe of the scatter diagram of the Brockley specimens (text-fig. 1*a*), though it falls within the range of variation of the Brockley specimens as shown by the histograms.

Table 2 shows a comparison of the neotype with the Brockley sample, in which the neotype is regarded as a sample of size 1, with mean values those of the neotype. Since t, difference between means/standard error of difference of means, does not exceed 1·96, the means do not differ significantly at the 5 per cent. level. The Brockley specimens are thus regarded as belonging to *Spirifer trigonalis*.

TABLE 2. *Comparison of the specimens from Brockley with the neotype of* Spirifer trigonalis (*Martin*)

Character	*Standard error of difference of means* $\sigma\sqrt{\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}$	$t = \frac{\text{Difference between means}}{\text{Standard error of difference of means}}$
$\frac{\text{Maximum width}}{\text{Length}}$	0·1938	1·34
$\frac{\text{Thickness}}{\text{Length}}$	0·0498	0·8
$\frac{\text{Number of ribs}}{\text{Length}}$	0·2975	1·02

DEVELOPMENT OF EXTERNAL FORM

The study of external growth-lines reveals changes in shell ratio (hinge width/length) during development. The shell becomes longer relative to its width in the later growth stages (text-fig. 3*a*). This change in growth ratio is found in both brachial and pedicle valves and in the interareas (text-fig. 3*b*). There is also some evidence of an opposite change in growth ratio during early growth stages.

There is considerable variation in the size and proportions of the shell of different individuals when the second change in growth ratio occurs; the width varies between 9·8 mm. and 25·2 mm. and the shell index between 1·5 and 2·1. The graph (text-fig. 3*c*) illustrates the growth of thirty-one specimens. In a few specimens no change occurs and extremely transverse shells are formed (pl. 64, fig. 14). These produce the skewness in the histograms (text-fig. 1*c*, *d*).

In contrast to the variable width/length ratio is the constant thickness/length ratio (text-fig. 1*b*) which is shown by the high coefficient of correlation (Table 1) and indicates an allometric relationship. Similarly, the ratio hinge width/number of ribs is constant both in the individual and in the collection as a whole (text-fig. 3*d*) except when dichotomy occurs.

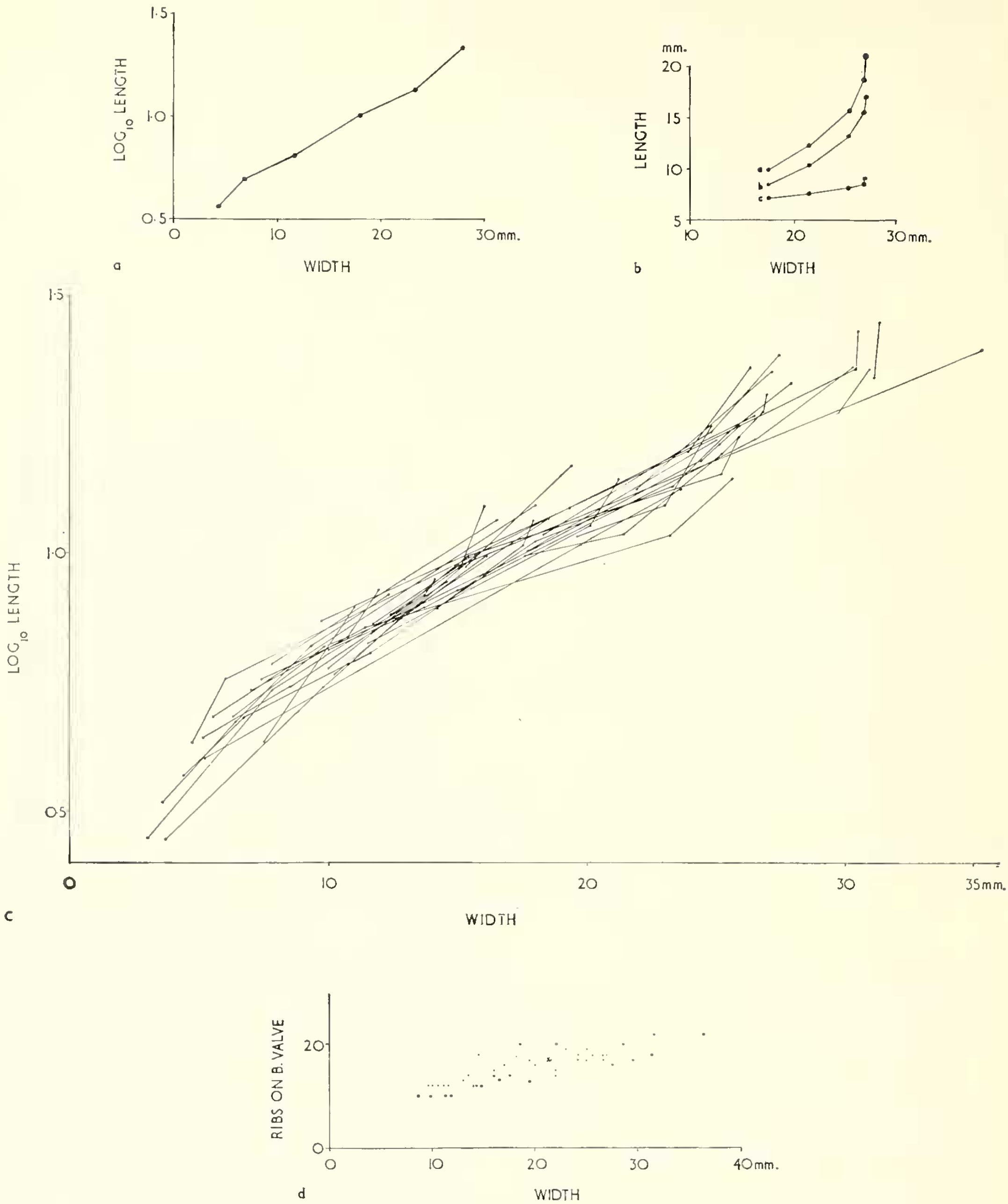
MICROSTRUCTURE OF THE SHELL

Terminology of shell layers. The shell is composed of three layers, all impunctate, the lamellar layer, the fibrous layer, and the columnar layer (text-fig. 4*a*).

Lamellar layer: this outer, non-fibrous layer, about 0·02 mm. in uniform thickness, extends over the whole surface of the shell.

Fibrous layer: immediately underlying the lamellar layer is the fibrous layer, of variable thickness, composed of long slender fibrous calcite crystals about 0·007 mm. in width. The fibres are perpendicular to the valve margins and are inclined inwards, in an anterior direction, at a low angle.

Some confusion exists about the naming of this shell layer. Thus, Williams (1953, p. 280) refers to the 'fibrous layer' while Cooper (1944, p. 281) uses the term 'prismatic layer' for the same structure. Carpenter (1853, p. 25), who first described this particular microstructure, states that 'the shell is found to consist of flattened prisms' but he does not refer to a 'prismatic layer'. Later, Hall (1867, p. 186) states simply that in *Spirifer*



TEXT-FIG. 3. Growth of the shell in *Spirifer trigonalis* (Martin). *a*, Graph of growth stages in one individual, showing a change in growth ratio at 24 mm. width. *b*, Graphs of growth stages in one individual—*a*, pedicle valve, *b*, brachial valve, *c*, ventral interarea. *c*, Graph of growth of the shell in 31 individuals showing changes in growth ratio during ontogeny. *d*, Scatter plot showing the direct relation between number of ribs and width of hinge in those specimens with no dichotomy of ribs. x=neotype of species.

'the shell substance is fibrous'. The indiscriminate way in which the terms have been used is illustrated in Schuchert's (1913, p. 357) discussion of shell structure. First he mentions a 'thick prismatic layer', then 'fibrous prisms', and finally, referring to the same structure, the 'fibrous layer'. With the description now of another type of prismatic layer in brachiopods, the columnar layer, it is preferable that the term fibrous layer be used for that microstructure in which the slender prisms are arranged at a low angle to the shell surface.

Columnar layer: this term is proposed for an inner prismatic layer which lies over the fibrous layer in some parts of the shell. It is of variable thickness and is composed of short, calcite prisms up to 1 mm. in length and 0·05 to 0·06 mm. in width (text-fig. 4*a*). The crystals are orientated normal to the shell surface and are elongate in this direction, which is the *c*-axis of the crystal. Their prismatic form is seen in tangential section (text-fig. 4*b*).

The columnar layer is frequently traversed by lines parallel to the surface of the shell (text-fig. 4*c*), marked in some cases by inclusions of a fine textured brown substance (pl. 65, fig. 1) and in other cases by cavities in the crystals. These discontinuities are considered to result from pauses in growth; the lines are regarded as growth-lines. They were recorded in Russian spiriferids by Miloradovitsch (1937, p. 526).

Relation of fibrous and columnar layers. The lamellar layer forms a thin film over the entire external surface of the shell and beneath it lies the fibrous layer, very thin at the umbones and increasing in thickness anteriorly. In contrast the columnar layer is confined to the posterior region (text-fig. 5*a*, *b*). Internal to the fibrous layer, it is distinctly separate from it, with no gradation between the two (text-fig. 5*c*). It is concluded that the columnar layer formed later than the fibrous layer, a distinct break occurring between the secretion of the two layers.

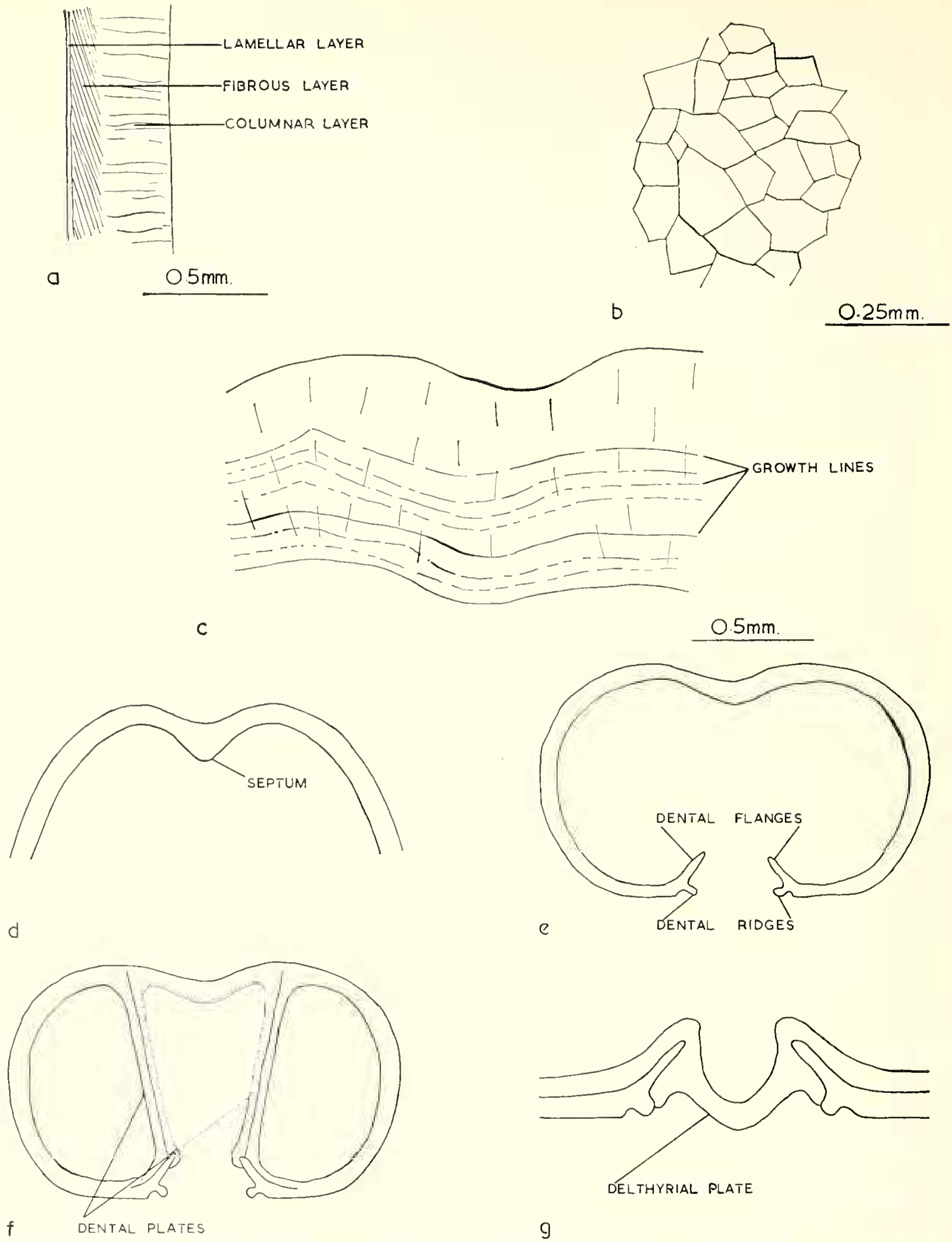
The columnar layer is present in shells not fully grown so its deposition was not merely a gerontic phenomenon. In the neanic shells its distribution is the same as in the adult shell. The deposition of the two types of shell material therefore occurred concurrently in different parts of the shell, the columnar layer gradually spreading anteriorly over the fibrous layer.

The fibrous layer continued to grow in thickness until it was covered by the columnar layer. Its thickest development therefore occurs immediately anterior to the columnar layer (text-fig. 5*a*). The columnar layer, on the other hand, continued to increase in thickness throughout growth and attains its maximum posteriorly.

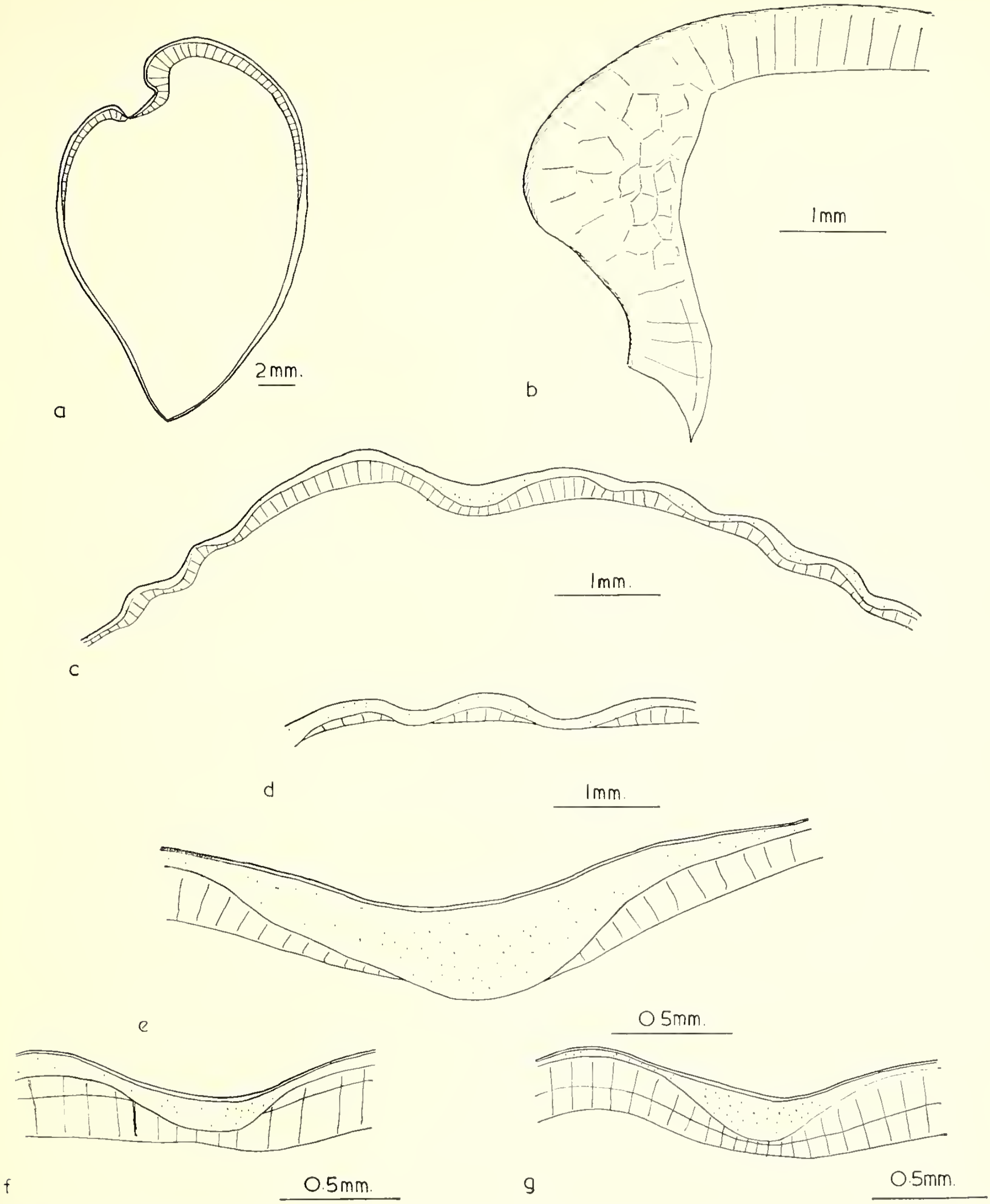
The fibrous layer, growing anteriorly, paralleled the margin of the valve and reflected all the undulations of the surface of the shell. The anterior margin of the columnar layer thus filled in the grooves before extending in an unbroken sheet across the width of the shell. This gradual infilling of the hollows is especially well seen on the flanks of the sulcus where the columnar layer tends to thin out against the fibrous layer before finally overlapping it (text-fig. 5*e*–*g*).

The columnar layer thus differs from the fibrous layer in its growth pattern.

In some cases the inner shell layers alternate with each other, fibrous layer occurring internal to columnar layer and columnar layer internal to that again (Pl. 65, fig. 4, text-fig. 6*a*). Rarely several alternations occur (text-fig. 6*d*). Such interlayering may occur in any part of the shell where columnar layer normally occurs, and while it is limited in



TEXT-FIG. 4. Microstructure of the shell and the internal plates of the pedicle valve of *Spirifer trigonalis* (Martin). *a*, Lamellar, fibrous, and columnar layers in longitudinal section. *b*, Columnar layer in tangential section. *c*, Columnar layer in transverse section, showing growth-lines. *d*–*g*, Internal plates of pedicle valves in transverse section; *d*, ventral septum; *e*, dental flanges and dental ridges; *f*, dental plates, dental flanges, and dental ridges; *g*, delthyrial plate, dental flanges, and dental ridges.



TEXT-FIG. 5. Distribution of shell layers in *Spirifer trigonalis* (Martin). *a*, Longitudinal section showing general distribution of fibrous and columnar layers. *b*, Longitudinal section of apex of pedicle valve showing columnar layer of umbonal infilling. *c*, Transverse section of young individual showing columnar layer in posterior part of shell. *d*, Transverse section showing anterior prolongations of columnar layer in the grooves on the inner surface of the shell beneath the ribs. *e*, Transverse section showing columnar layer flanking the fibrous layer of the sulcus. *f*, Transverse section showing columnar layer overlapping the fibrous layer of the sulcus. *g*, Transverse section showing columnar layer thinning against and overlapping the fibrous layer of the sulcus.

longitudinal extent to some 5 mm. it stretches right across the valve. It is clear that in certain circumstances fibrous layer may have been secreted over columnar layer.

The columnar layer may occur only as lenticles in the fibrous layer (text-fig. 6*b*). In this case the renewed secretion of fibrous layer had occurred in an area where the columnar layer only occupied the hollows of the ribs.

The particular conditions governing the development of interlayering are discovered when the repeated layers are traced anteriorly and posteriorly (text-fig. 7*c*, *d*). Anteriorly the outer columnar layer dies out and two sheets of fibrous layer come together separated by a plane of discontinuity in the fibres. When this plane is traced to the surface (Pl. 65, fig. 6, text-fig. 7*d*) it is found to correspond with an external growth-line. Similarly, when the inner fibrous layer is traced posteriorly from the zone of interlayering it dies out and is replaced by an internal growth-line in the normal layer. Interlayering is therefore consequent on a pause in the growth of the shell.

A growth halt which produced a prominent external growth-line also affected the internal secretion of the shell material. A discontinuity of structure can be traced from the external growth-line posteriorly to the umbo (text-fig. 7*b*); anteriorly the break occurs within the fibrous layer, posteriorly the break is in the columnar layer and between the two is the zone of interlayering. The interareas also display a narrow zone of interlayering (text-fig. 7*e*). The growth halt is thus recorded in various ways in all parts of the shell.

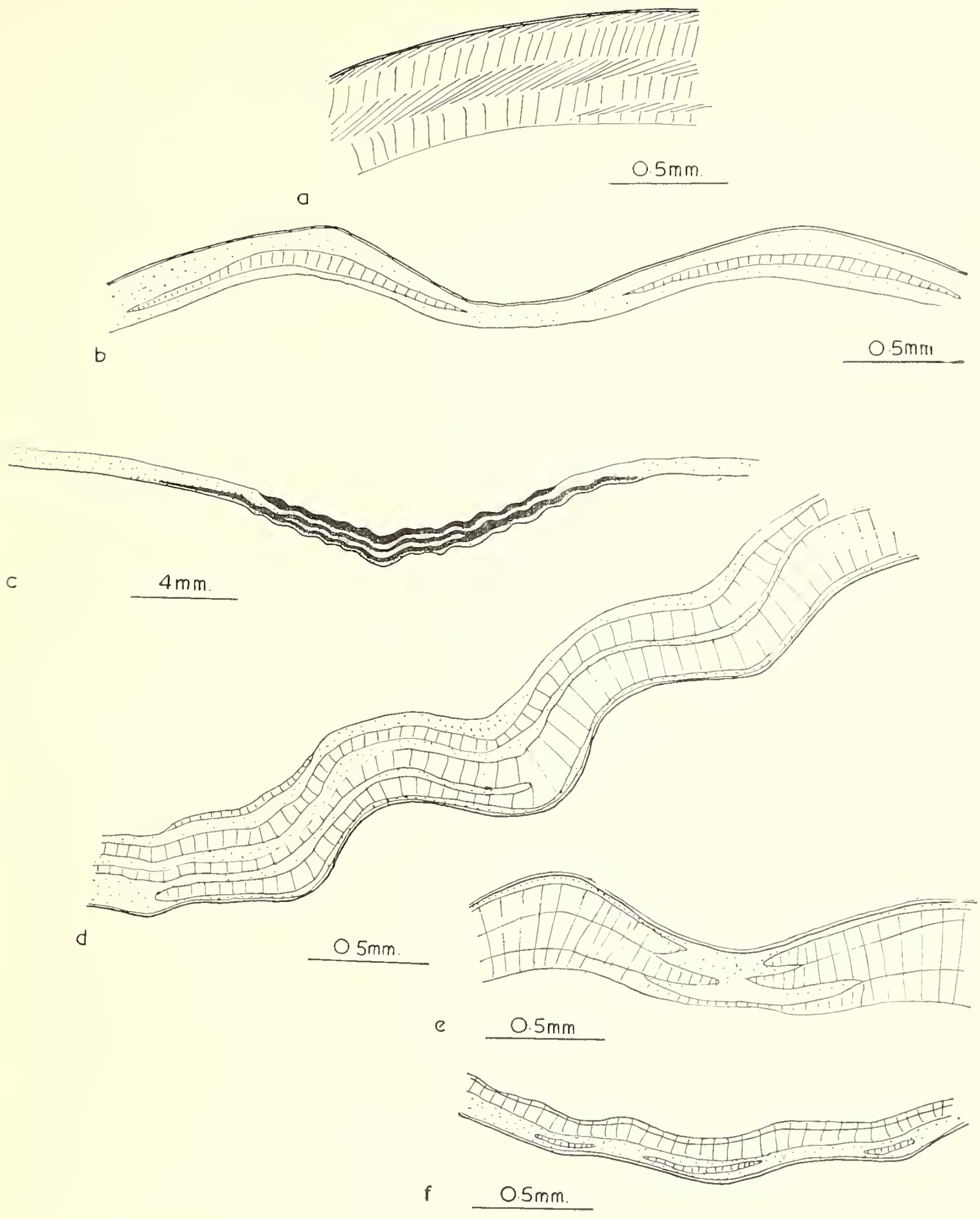
Growth pauses may occur at any stage in the development of the shell, the early ones being recorded only in the posterior parts of the shell. In transverse sections, therefore, the older median part may record more pauses than the younger lateral parts (text-fig. 6*c*, *d*).

Late-stage intermittent growth, often found in larger specimens, did not cause any considerable interlayering, though duplication of the fibrous layer anteriorly, and growth-lines in the columnar layer posteriorly, are observed.

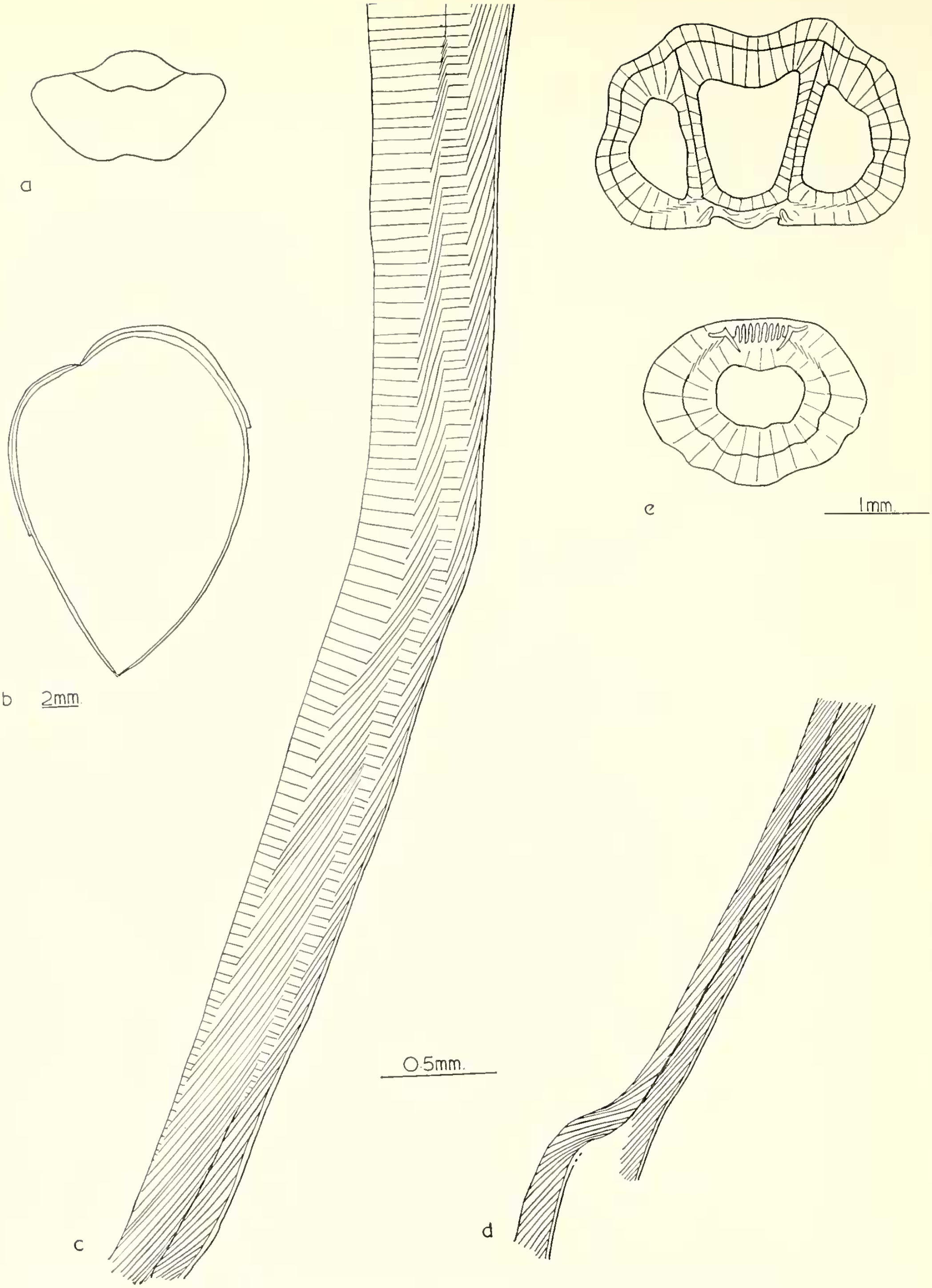
Mode of formation of fibrous and columnar layers. Since the columnar and fibrous layers differ in their structure and in their pattern of development it seems probable that they were deposited by different parts of the mantle. Williams (1956, p. 246) shows that the secondary (=fibrous) layer forms at the mantle edge and increases in thickness with growth. Its secretion is intracellular, each fibre having a corresponding epithelial cell. The columnar layer clearly did not form at the mantle edge, and the larger dimensions of its crystals indicate that the mantle secreting it was of a different form from that secreting the fibrous layer. Williams (1956, p. 250) considers that an inner layer of this type is formed by extracellular secretion.

The reason for the modification of the mantle posteriorly is not known. Though the columnar layer corresponds in area with the viscera it seems unlikely that there was any genetic relation between the viscera and the columnar layer since most brachiopods and many spiriferids are devoid of columnar layer.

The interlayering of the shell suggests that the same part of the mantle could secrete both types of shell material, yet the mantle secreting fibrous layer was apparently structurally different from that secreting columnar layer. To produce interlayering, the mantle would be required to change in structure repeatedly. The interlayering, however, only developed after a growth halt and the formation of fibrous layer on columnar layer



TEXT-FIG. 6. Interlayering of columnar and fibrous layers in the shell of *Spirifer trigonalis* (Martin). *a*, Longitudinal section showing two interlayerings of fibrous and columnar layers. *b*, Transverse section showing two 'lenticles' of columnar layer in fibrous layer. *c*, Transverse section showing several interlayerings (columnar layer black). *d*, Enlargement of part of fig. *c*, showing four fibrous and four columnar layers. *e*, Transverse section of ventral sulcus showing interdigitation of fibrous and columnar layers. *f*, Transverse section of dorsal fold of the same specimen as in fig. *e*, showing a corresponding development of 'lenticles' of columnar layer.



TEXT-FIG. 7. Modification of the shell of *Spirifer trigonalis* (Martin), due to a growth pause. *a*, External view showing one prominent growth-line. *b*, Longitudinal section of the same specimen showing the corresponding internal growth-line. *c*, *d*, Longitudinal section with detailed microstructure showing interlayering of fibrous and columnar layers, growth-lines in both columnar and fibrous layers, external growth-line, and interruption of lamellar layer. *e*, Transverse sections through the apices of both valves showing a growth-line in columnar layer and interlayered fibrous layer in the interareas.

would appear to result instead from a contraction of the mantle which brought that part of the mantle responsible for the secretion of fibrous layer over an area in which columnar layer had been deposited before the growth halt (text-fig. 8).

Since the secretion of the fibrous layer is intracellular a contraction of the mantle would have caused disruption of the epithelial cells. This is apparently borne out by the complete lack of correspondence of the fibres of the fibrous layer across the growth line (text-fig. 7*d*). In the columnar layer, on the other hand, there is continuity of crystal structure across the growth-lines, but this does not imply absence of mantle contraction since the prisms would develop in crystallographic continuity as long as secretion was extracellular.

The amount of contraction of the mantle would be variable depending probably on the duration of the growth pause. It is measured by the length of the zone of interlayering which it produced. The maximum observed is 5 mm. It is possible that greater contraction occurred, for the epithelial cells may be rendered incapable of further secretion and then the generative zone, close to the mantle edge, would have had to be brought back into the shell in a position corresponding to the posterior end of the inner oblique layer. This is an observed maximum of 8 mm.

INTERNAL MORPHOLOGY OF THE SHELL AND ITS DEVELOPMENT

Terminology of internal plates. Median septum (text-fig. 4*d*): any plate in the longitudinal, median plane of either valve is referred to as a median septum.

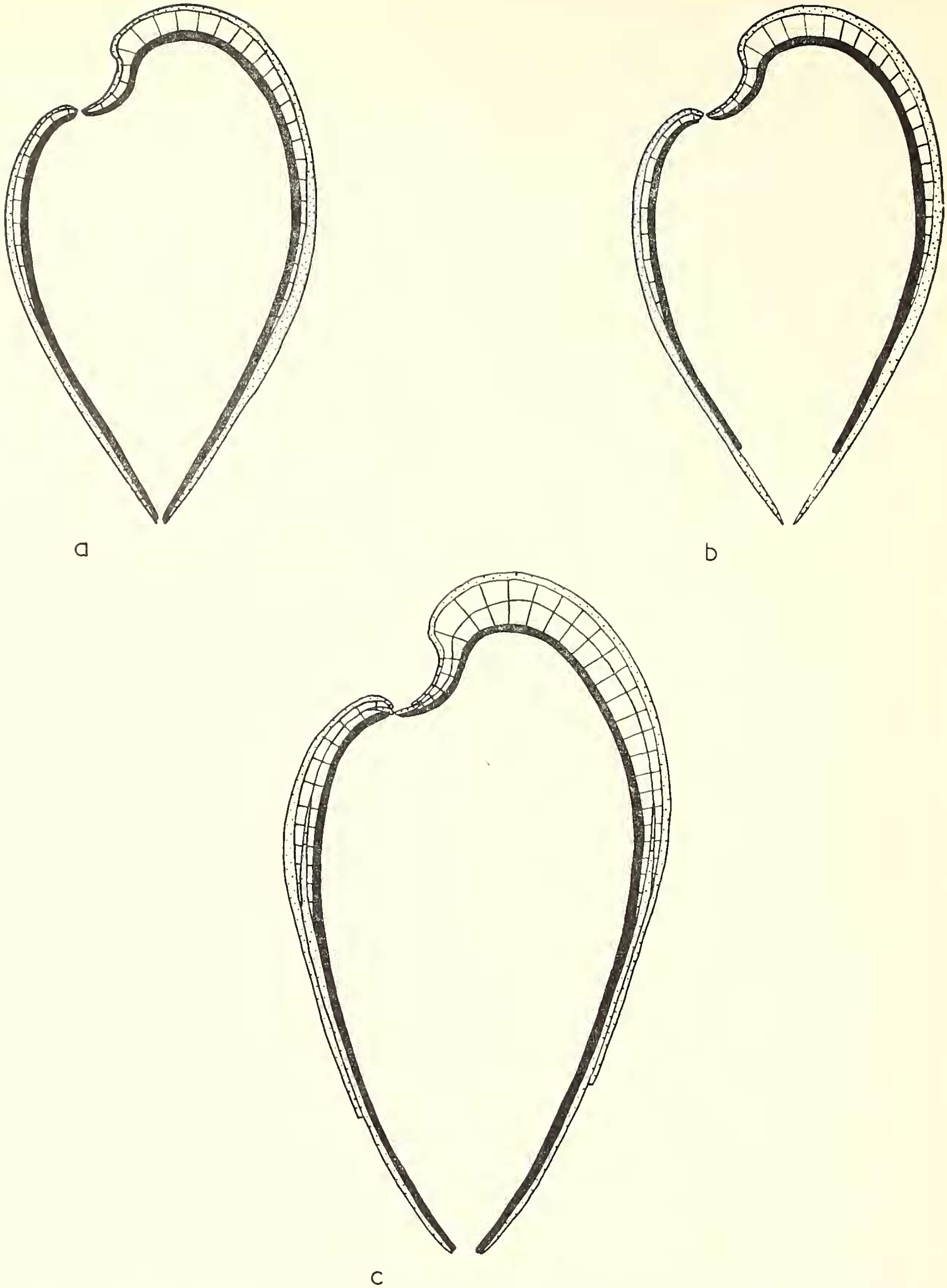
Dental plates (text-fig. 4*f*): this term, first used by King (1850, p. 68), refers to two vertical plates which project from the delthyrial margins, across the apical cavity, to the floor of the valve.

Dental ridge (text-fig. 4*e*): Alexander (1948, figs. 3*f* and 6*a*) refers to the ridge along the delthyrial margin in pentamerids as a dental ridge. The ridge represents the successive growth stages of the hinge tooth. Cooper (1954, p. 328) refers to the same structure in spiriferids as 'the growth track of the tooth'. Alexander's term is adopted here.

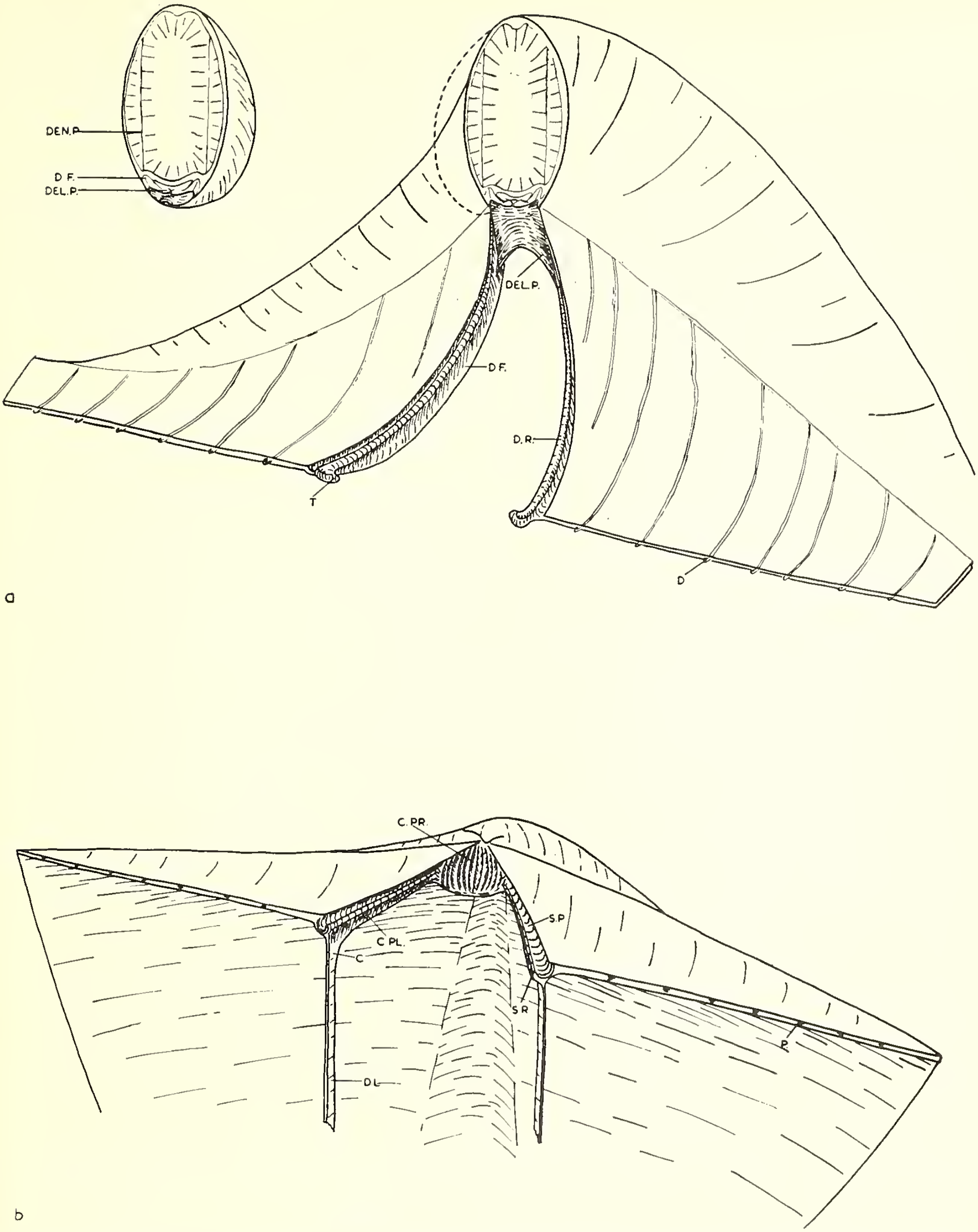
Dental flange (text-fig. 4*e*): this is a new term proposed for a subsidiary dental structure. The dental flange is a projecting plate on the inner side of the dental ridge. It extends along the length of the dental ridge and is directed into the delthyrial cavity, making an obtuse angle with the interarea. The two flanges, on either side of the delthyrium, are thus convergent. For part of its length the dental flange is buried within the dental plate (text-fig. 4*f*).

Delthyrial plate (text-fig. 4*g*): several terms have been used to describe the plate which extends across the delthyrium, between the dental plates, closing the delthyrium at the apex and extending anteriorly to a greater or less extent. Hall (1867, pp. 248 and 254) uses transverse septum, Hall and Clarke (1894, p. 29) use transverse plate, Cooper (1954, p. 328), Stainbrook (1943, p. 421), and Miloradovitsch (1937, fig. 16) use transverse delthyrial plate, Fredericks (1927, p. 3) simply uses delthyrial plate. Fredericks's term is adopted.

Methods of interpretation of development. Three lines of evidence are used in tracing the development of the internal structures of the shell. Firstly, direct evidence is derived from a comparison of young and old specimens. Secondly, the sequence of development



TEXT-FIG. 8. Hypothetical reconstruction of the mantle in *Spirifer trigonalis* (Martin). Mantle is shown in solid black. *a*, Shell before a growth halt with mantle in normal position. *b*, Shell during a growth halt with mantle retracted. *c*, Shell after a growth halt showing interlayering of the shell and readvance of mantle. (Approximately $\times 4$.)



TEXT-FIG. 9. Reconstruction of the apices of the valves of *Spirifer trigonalis* (Martin). *a*, Pedicle valve with umbo inset. *b*, Brachial valve. Abbreviations in this and subsequent text-figures: den. p., dental plate; del. p., delthyrial plate; d.f., dental flange; d.r., dental ridge; t., tooth; d., denticle; c., crus; c. pl., crural plate; c. pr., cardinal process; d.l., descending lamella; s.r., socket ridge; s.p., socket plate; p., pit.

can be proved in some parts of the shell where later structures are superimposed on early structures without any resorption of the previous shell substance. Thirdly, the shell layers show growth-lines which illustrate the form of particular parts of the shell at successive stages in growth.

The pedicle valve. The dental ridges and dental flanges lie along the delthyrial edges; the dental plates fall from the margins of the delthyrium to the floor of the valve where the median septum rises; the delthyrial plate, supported between the dental flanges, closes the delthyrium for about a quarter of its length (text-fig. 9*a*). Enveloping all these structures to some extent is the apical infilling, a development of columnar layer ('callus') on the inner surface of the umbo (text-fig. 9*a* inset).

The extreme apex of the valve is without dental ridges, flanges and plates (text-fig. 11*o*).

Thus, at the earliest stage which can be inferred, the pedicle valve was gently convex, with an open delthyrium, and was composed of lamellar layer and fibrous layer. With growth, the fibrous layer thickened away from the umbo, and, even at a young stage, was succeeded by columnar layer.

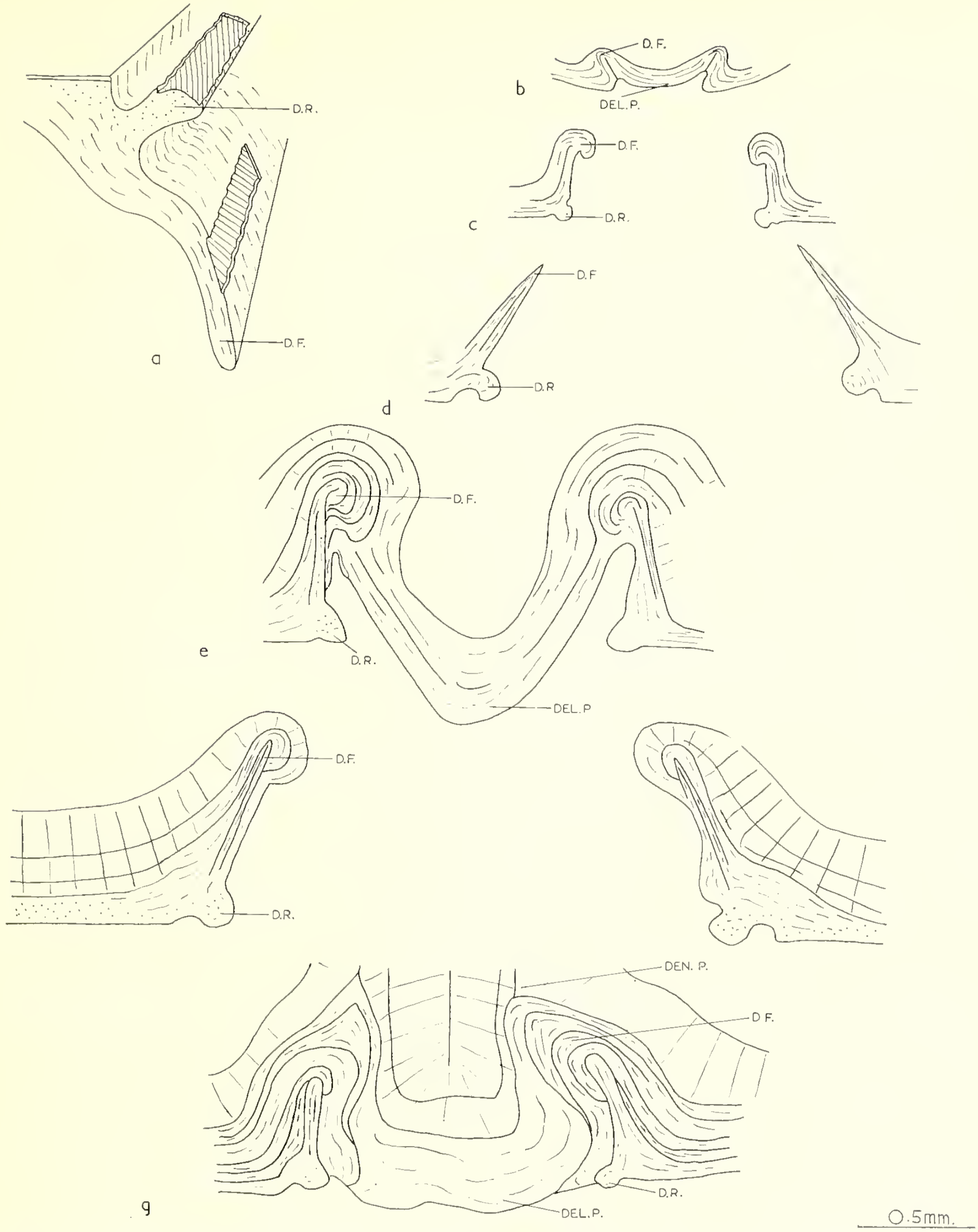
Dental ridges and dental flanges: the dental ridges appear about 0·5 mm. from the umbo (text-fig. 10*c*). Subcircular in transverse section, they increase in size anteriorly to a diameter of about 0·25 mm. They are separated from both the interarea and the dental flanges by grooves (text-fig. 10*a*). The dental flanges appear slightly posterior to the dental ridges (text-fig. 10*b*) and extend along the inner surface of the ridges. They increase in width to about 1 mm. close to the cardinal margin, before dying out just short of the teeth. Anteriorly the flange has an angular inner edge (text-fig. 10*d*), but as it is traced posteriorly its form changes, so that at mid-length the inner edge is curved over and a low ridge is formed on the outer surface of the flange (text-fig. 10*c*).

Both dental ridges and dental flanges are composed of fibrous layer and where flange and ridge come in contact the fibres are intergrown (text-fig. 10*a*). In the ridges the crystals lie normal to the hinge-line, and intersect the edges of the ridges. In the flanges a distinct median plane divides the fibrous layer into two sheets which merge along their inner edges. The fibres lie normal to the length of the flange and parallel to the median plane, never crossing it (text-fig. 10*d*).

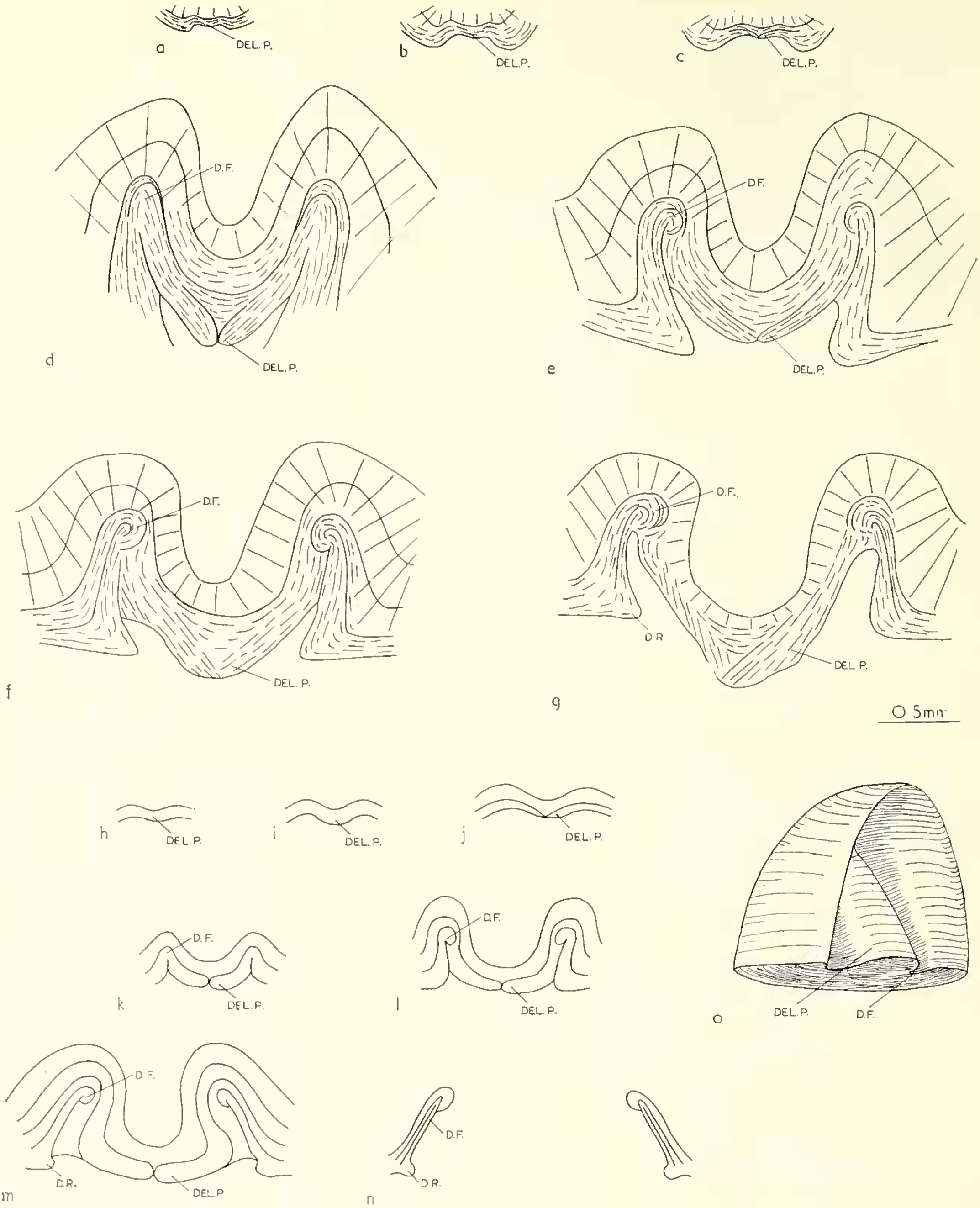
From the double structure of the dental flanges it is inferred that they, together with the dental ridges, were secreted by two small mantle folds bordering the delthyrium. The later development of the flanges is seen in the adult shell where several successive layers can be recognized in each flange. These are best developed on the inner surface where they consist in large part of columnar layer. The form of the flange, in some cases, was changed at this stage, a curved flange forming around a small angular-edged one (text-fig. 10*f*).

Delthyrial plate: throughout its length the delthyrial plate is convex, and anteriorly the convexity is sufficient to bring the plate above the level of the delthyrium (text-fig. 11*g*). Its free margin is concave. Columnar layer is present on the inner surface, but much of the plate is formed by fibrous layer, the fibres lying parallel to the surface and oblique to the length of the plate (text-fig. 11*a–g*).

Since the delthyrial plate consists only of fibrous and columnar layers, no lamellar layer extending on to it from the interarea, it is considered to be an internal structure which was covered by the mantle throughout life (cf. Williams 1953, p. 280). It would



TEXT-FIG. 10. Dental flanges and dental ridges in *Spirifer trigonalis* (Martin). *a*, Reconstruction of dental ridge and dental flange, dissected to show the orientation of the fibres (×60). *b–d*, Three transverse sections through apex of delthyrium. Section interval 0·05 mm. *b*, Dental flanges and delthyrial plate; *c*, *d*, dental flanges and dental ridges. *e–f*, Two transverse sections, 1·25 mm. apart. *e*, Multi-layered dental flanges with delthyrial plate and dental ridges; *f*, multi-layered dental flanges and dental ridges. *g*, Multi-layered dental flanges and delthyrial plate covered by bases of dental plates.



TEXT-FIG. 11. Delthyrial plate in *Spirifer trigonalis* (Martin). *a–g*, Transverse sections of the structures at the apex of the delthyrium, section interval *a–b*, 0·10 mm., *b–c*, 0·05 mm., *d–e*, 0·05 mm., *e–f*, 0·15 mm., *f–g*, 0·30 mm., showing development of delthyrial plate and emergence of dental flanges. *h–n*, Diagrammatic representation of development of delthyrial plate and dental flanges (×20). *o*, Reconstruction of umbo of pedicle valve showing delthyrial plate arising from floor of valve a short distance from umbo. (Approximately ×25.)

have been formed within a mantle fold which rose from the floor of the valve a short distance from the umbo, crossed the apical cavity to the delthyrium, and bent back on itself to the floor of the valve (text-fig. 11*o*). In this way, not only would the delthyrial plate have been initiated, but the infilling of the apical cavity would also have begun. This mantle fold would be flanked by the two smaller folds in which the dental ridges and flanges would be secreted.

Apically the structure of the dental flanges merges with that of the delthyrial plate (text-fig. 10*b*), and at the summit of the delthyrium the flanges are rudimentary, not distinctly separable from the plate (text-fig. 11*a*, *b*). Initially then the delthyrial plate and its flanking dental flanges formed simultaneously (text-fig. 11*h*, *i*). But, anteriorly, a median parting of fibres develops in the outermost layer of the plate (text-fig. 11*c*, *d*, *e*, *j*, and *k*), minor discontinuities form laterally (text-fig. 11*f*), and finally the dental flanges appear as discrete structures from which the delthyrial plate is suspended (text-fig. 11*l*). It seems then that the lateral parts of the mantle fold grew in advance of the median part. Sometimes a considerable interval would elapse between the appearance of the dental flange and the secretion of the delthyrial plate, for there are several successive layers in the flange beneath the delthyrial plate (text-fig. 11*m*). Anteriorly the dental flanges completely outstrip the delthyrial plate and the anterior part of the delthyrium remains open (text-fig. 11*n*).

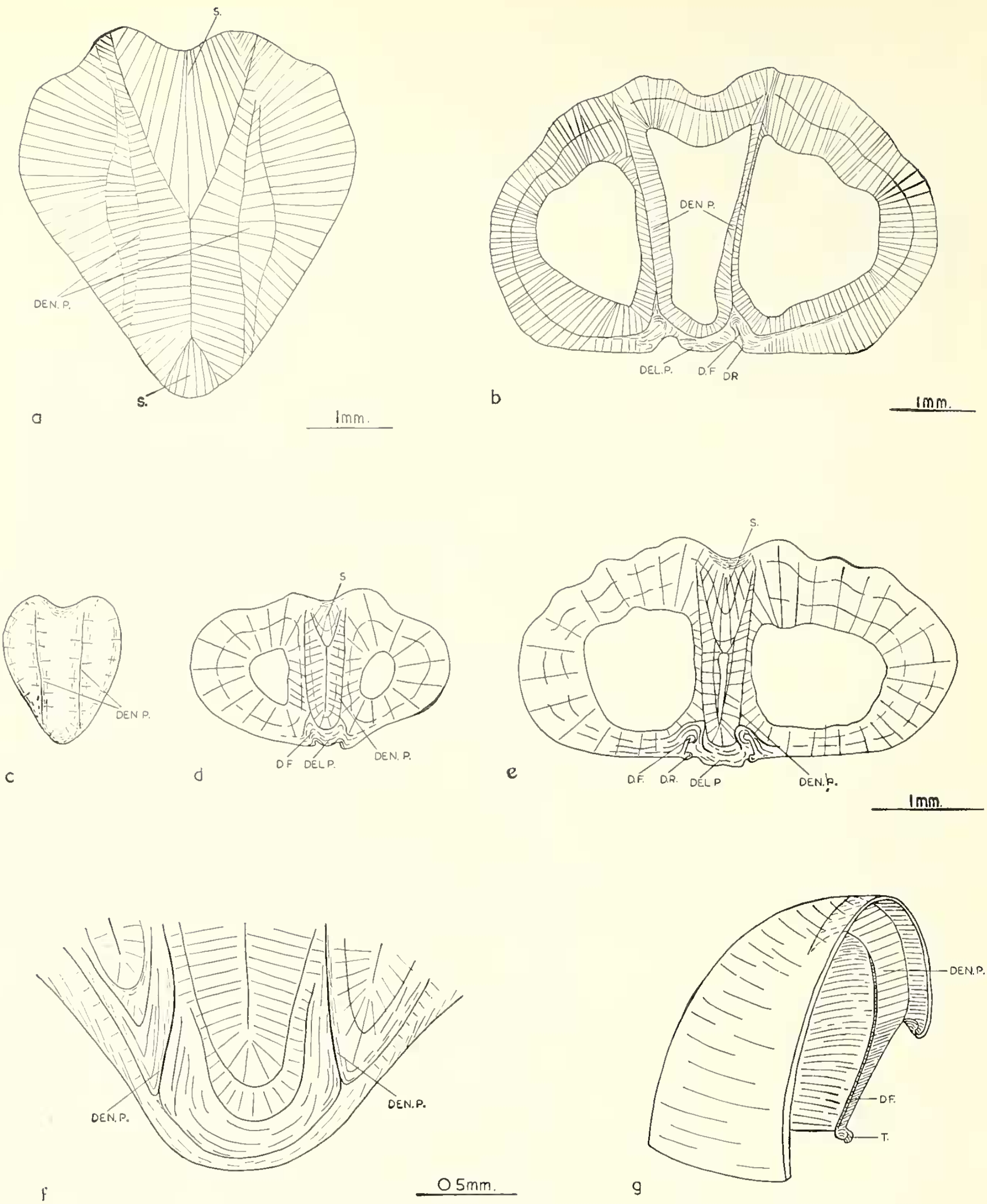
There is no indication that any secretion took place on the outer surface of the delthyrial plate after its formation, though it is assumed that it remained enveloped by mantle since no lamellar layer is present on it. The plate grew in thickness internally. This is in contrast to the dental flanges in which secretion continued on both outer and inner surfaces, though the inner growth greatly exceeds the outer.

Median septum: at approximately 0·5 mm. from the tip of the umbo a low, narrow, median ridge rises on the floor of the pedicle valve and extends for about a third of the length of the valve, widening anteriorly. Beneath the septum there are, in some cases, unfolded layers of the shell wall. It is thus inferred that, when the shell had become somewhat thickened, and while the structures just described were forming around the delthyrium, the median septum was secreted by a fold of the mantle on the floor of the valve.

Dental plates: the dental plates extend along the margins of the delthyrium, posteriorly from the teeth, but whereas the delthyrial margins converge, the dental plates become nearly parallel posteriorly and never reach the umbo (text-fig. 12*c*–*e*). They cross from the interarea to the floor of the valve some little distance anterior and lateral to the umbo (text-fig. 12*g*). Their position relative to the dental flanges is thus variable along their length (text-figs. 12*b*–*e*). They show much variation in length, but commonly extend a very short distance on the floor of the valve (text-fig. 12*g*).

The dental plates are formed almost entirely of columnar layer. Each plate is made up of two parts, the surface separating the parts appearing in section as a well-defined line (text-fig. 12*b*). The crystals do not cross this line, usually meeting it at an angle. It is deduced from their double structure that the dental plates were formed within two parallel longitudinal invaginations of the mantle which extended from the delthyrium across the apical cavity to the floor of the valve, each side of a plate being formed by secretion from one side of a fold.

The two dental plates divide the apex of the valve into three chambers, a central



TEXT-FIG. 12. Dental plates in *Spirifer trigonalis* (Martin). *a*, Section through the incurved umbo passing twice through the septum. The dental plates, completely filling the umbo, are in contact with the septum. *b*, Transverse section showing the dental plates forming the apical cavities and enveloping the dental flanges. *c–e*, Three transverse sections, section interval *c–d*, 1·2 mm., *d–e*, 0·8 mm., showing the parallelism of the dental plates and their variable position relative to the dental flanges. *f*, Transverse section in the apex of the pedicle valve showing the thin shell layer external to the base of the dental plates. *g*, Reconstruction of the apex of the pedicle valve illustrating the parallelism of the dental plates posteriorly, their divergence along the delthyrial margin, and absence at the umbo. (Approximately $\times 5$.)

delthyrial cavity and two lateral umbonal cavities. Each cavity is lined with columnar layer which passes with slight discordance into the columnar layer of the dental plates (text-fig. 12*b*, *d*, *e*). The columnar layer in these cavities may be so thick apically that it fills the cavity; the dental plates are only recognized by the trace of the line of junction in each plate (text-fig. 12*c*) and the median septum is represented by a triangular wedge between the plates (text-fig. 12*a*).

The formation of the dental plates occurred after the thickening of the shell had proceeded to some extent, for the bases of the dental plates do not extend to the outer shell layers (Pl. 65, fig. 4; text-fig. 12*f*). In some cases the dental plates formed simultaneously with the median septum for growth-lines can be traced from the dental plate round the delthyrial cavity and across the septum (text-fig. 12*e*). In other cases the dental plates developed after the septum and completely enveloped it.

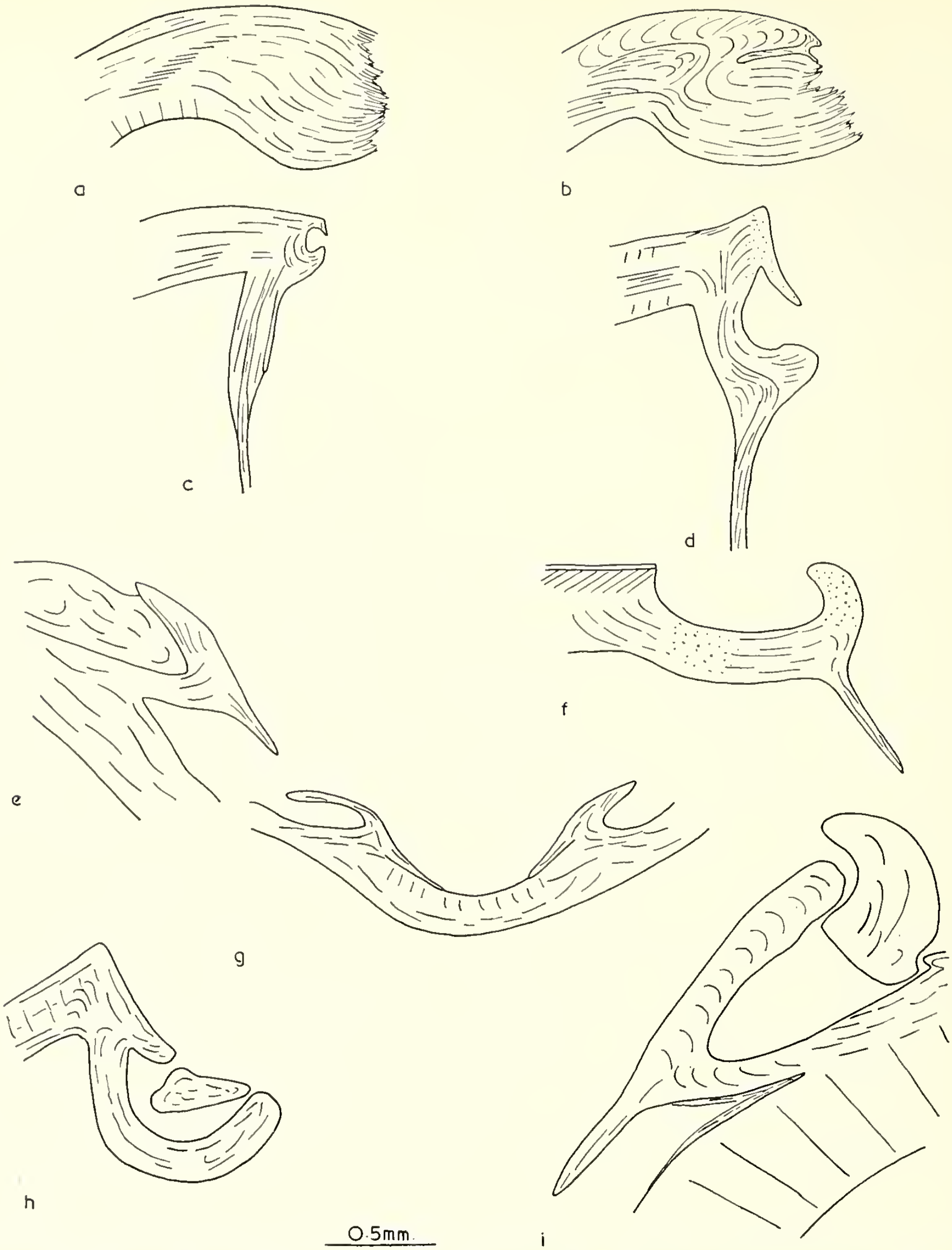
Further information about the stage at which the dental plates developed is obtained from young specimens. These possess dental ridges, dental flanges, and a delthyrial plate but are devoid of dental plates, showing that the dental plates developed later than these other structures. The same conclusion can also be drawn from the way that the dental plates grow over the dental flanges. Indeed it might seem that the dental flange was no more than an immature dental plate which was not long enough to reach the floor of the valve, but grew later into a full dental plate. However, this is not so, for the dental plates and dental flanges do not always correspond exactly in position, the delthyrial margins converging, and the dental plates remaining almost parallel (text-fig. 12*c*–*e*). The dental plates appeared as a new element in the ephebic shell; they did not develop out of a structure present in the neanic stages.

In at least one specimen the development of the dental plates took place immediately after a growth halt. The interruption in growth is recorded in the columnar layer of the apical chamber as a prominent growth-line. The dental plates are in continuity with the columnar layer within the growth-line, showing that the plates were secreted after the interruption of growth (text-fig. 12*b*).

At their youngest observed stage the dental plates form two relatively long ridges which extend from the delthyrium to the floor of the valve across the apex of the valve. At this stage they are not partitions, only low ridges. They are of uniform height suggesting that growth commenced simultaneously along their length, rather than extending gradually from a point. The position of the new dental plates in relation to the delthyrium corresponds with the position of the dental flanges immediately anterior to the delthyrial plate. The invaginations of the mantle in which the dental plates were secreted apparently formed in continuity with the mantle folds surrounding the dental flanges, where these became free from the delthyrial plate. Indeed, in their anterior prolongations the dental plates splay out along the delthyrial margins and are inseparable from the dental flanges.

As growth proceeded the low ridges of the dental plates developed into complete partitions in the apical cavity; they increased in thickness as the valve wall increased, till together they formed the apical infilling; and, as the dental flanges became thicker and the delthyrial plate grew anteriorly between them, the dental plates too extended anteriorly, growing around the dental flanges and resting on the delthyrial plate with their bases between the dental flanges.

The material infilling the umbo, essentially columnar layer, is commonly referred to as the 'umbonal callus' and dismissed as a late-stage infilling of no great significance.



TEXT-FIG. 13. Dental sockets in *Spirifer trigonalis* (Martin). *a–d*, Four longitudinal sections through the cardinal process and dental sockets. Section interval, *a–b*, 0·1 mm., *b–c*, 0·6 mm., *c–d*, 0·4 mm. *a*, Sagittal section showing irregular surface of cardinal process; *b*, early formed dental socket and crus within cardinal process; *c*, dental socket and crus emerging from cardinal process; *d*, dental socket with overhanging interarea and descending lamella attached to convex surface. *e*, Transverse section showing dental socket infilled by later material. *f*, Transverse section of dental socket with well-developed socket ridge and crural plate attached to convex surface of socket. *g*, Transverse section showing crural plates fused to the floor of the valve. *h*, Tooth and socket in longitudinal section. *i*, Tooth and socket in transverse section.

The apical infilling, intimately connected with the dental plates and other delthyrial structures, is as much a part of the shell as the outer layers, and it is to be regarded as reflecting a stage in the formation of the shell no less important than that preceding it.

The brachial valve. At the earliest growth stage which can be inferred, the brachial valve like the pedicle valve was formed of lamellar layer and fibrous layer and was without internal plates. As growth proceeded the fibrous layer became thicker, and at the umbo the formation of the cardinalia was initiated.

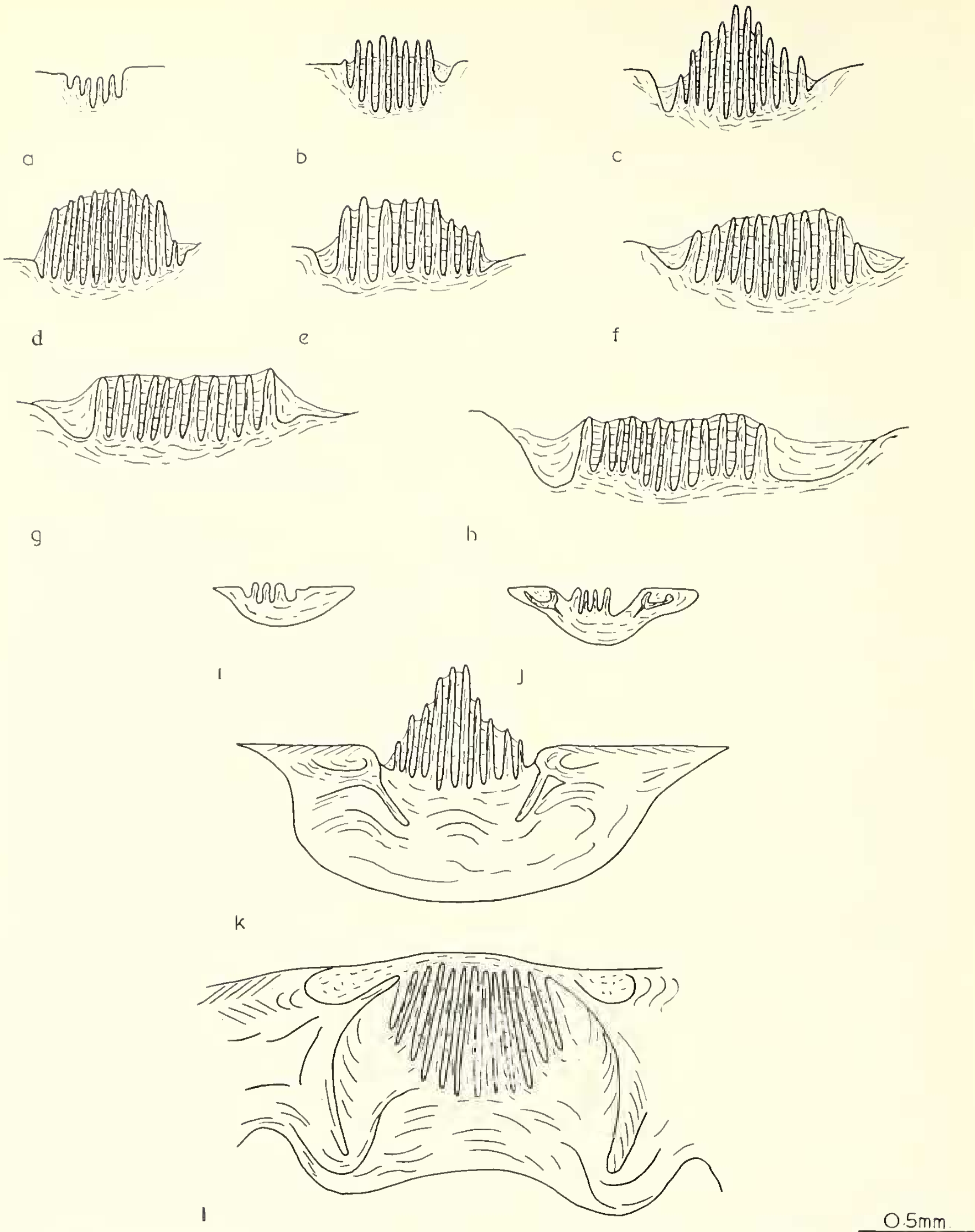
Dental sockets: the curved plates of the dental sockets extend along the inner margins of the notothyrium from about 0·1 mm. from the umbo to the hinge-line and project a little into the pedicle valve (text-fig. 9*b*). The sockets are larger and deeper anteriorly (text-fig. 13*b–d*) and their inner edges are turned up to form inner socket ridges (text-fig. 13*f*). The overhanging edge of the interarea functions as an outer socket ridge (text-fig. 13*d*). Both the sockets and the interarea are formed by fibrous layer but the structure of each is distinct: the fibres in the interarea lie along its width, inclined inwards, away from the notothyrium; those in the socket lie in the longitudinal plane and curve around the socket (text-fig. 13*d*, *f*).

Crura and crural plates: the crura are attached along the convex under surface of the dental sockets (text-fig. 13*d*). Their descending lamellae, about 0·75 mm. in width, parallel with the notothyrial margins, extend almost to the anterior margin before rotating into a plane parallel with the width of the shell and giving rise to the spiralia. The crural plates extend along the length of the dental sockets and anteriorly are continuous with the crura (text-fig. 9*b*). They increase in width anteriorly from 0·3 mm. to 1·3 mm. and, due to the spiral growth of the shell, change in inclination along their length through an angle of about 90° (text-fig. 13*b–d*). It is inferred that the dental sockets and crural plates were secreted by two mantle folds extending along the notothyrium; and the crura and spires, formed in structural continuity with the dental sockets, were secreted by two offshoots of the mantle folds. There is no indication of successive layers within the socket or crural plates, so they did not increase in thickness with growth. As the socket plates extended during the growth of the shell, the early sockets were abandoned, and were later infilled.

The earlier-formed descending lamellae of the crura are not preserved and there is no trace of any but the latest stage in the development of the spires. It is concluded that the spires and descending lamellae were continually resorbed and grown again; only the crural bases remain intact, later enveloped in the cardinal process.

Cardinal process: the cardinal process is of the striate type usual in spiriferids (text-fig. 9*b*). It is situated at the apex of the notothyrium and spreads laterally to envelop the posterior parts of the socket and crural plates (text-figs. 13*a*, 14*k*). The earliest-formed part of the cardinal process is at the apex of the notothyrium, where no dental sockets are present (text-fig. 14*i*). It may therefore have been formed earlier than the sockets, but it is more probable that it was formed at the same time as the sockets though slightly posterior to them.

It is composed entirely of fibrous layer, the dorso-ventrally elongate fibres giving rise to a smooth lower surface and an irregular upper surface where the ends of the fibres are free (text-fig. 13*a*). This upper surface is the area of muscle attachment. The fibres are in continuity with those of the fibrous layer of the shell wall, only a flexure of the fibres



TEXT-FIG. 14. Cardinal process in *Spirifer trigonalis* (Martin). *a–h*, Series of transverse sections, section intervals *a–b*, 0·12 mm., *b–c*, 0·08 mm., *c–d*, 0·05 mm., *d–e*, 0·05 mm., *e–f*, 0·05 mm., *f–g*, 0·10 mm., *g–h*, 0·03 mm., showing the anterior increase in number of plates in cardinal process. *i–j*, Transverse sections through the cardinal process of a young individual. *k*, Cardinal process and flanking dental sockets and crural plates attached to the valve floor by later shell growth. *l*, Stages in the envelopment of the crural plates shown by growth-lines. The dental sockets and grooves in the cardinal process both infilled.